

THE MONOTYPIC GENERA OF CICHLID FISHES IN LAKE VICTORIA, PART II¹

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A REVISION of the four endemic monotypic cichlid genera of Lake Victoria, *Macropetreodorus bicolor* (Blgr.), *Platytaeniodus degeni* Blgr., *Hoplotilapia retrodents* Hilg., and *Paralabidochromis victoriae* Greenwood has already been published (Greenwood, 1956). These species differ from *Haplochromis* in various dental characters. Unlike the other monotypic genera, *Astatoreochromis alluaudi* is not confined to the Lake Victoria basin; its range includes Lakes Edward, George, Nakavali and Kachira (Trewavas, 1933). Furthermore, *Astatoreochromis* differs from *Haplochromis* only in having an increased number of spines in the anal fin; the oral dentition is typically that of a non-piscivorous *Haplochromis*.

Genus *ASTATOREOCHROMIS* Pellegrin, 1903

Astatoreochromis Pellegrin, 1903, *Mém. Soc. zool. France*, **16**, 385; *Idem*, 1905, *ibid.* **17**, 185, pl. XVI, fig. 2; *Idem*, 1910, *ibid.* **22**, 297; Regan, 1922, *Proc. zool. Soc., London*, 188; Fowler, 1936, *Proc. Acad. nat. Sci. Philad.* **88**, 333, fig. 138 (mis-spelt *Astatore*); Poll, 1939, *Explor. Parc. Nat. Albert, mission H. Damas* (1935-36), fasc. 6, 1-73. *Haplochromis* (part) Boulenger, 1907, *Fish, Nile*, 505 pl. XC, fig. 4; *Idem*, 1911, *Ann. Mus. Genova* (3), **5**, 71; *Idem*, 1915, *Cat. Afr. Fish.* **3**, 305, fig. 206.

Type species. *Astatoreochromis alluaudi* Pellegrin, 1903.

Diagnosis. *Astatoreochromis* differs from *Haplochromis* only in having four or more spines in the anal fin. From other genera in the *Haplochromis* group with more than four anal fin spines, *Astatoreochromis* is distinguished by the absence of a marked antero-posterior differentiation in the form of the premaxillary teeth.

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In comparison with the *Haplochromis* of Lakes Victoria, Edward, and Kachira, *Astatoreochromis* shows an increased ratio of spinous to branched rays in the dorsal and anal fins. From other *Haplochromis*-like genera in these lakes, *Astatoreochromis* differs both in having more anal fin spines and in the nature of its oral dentition.

Discussion. As Boulenger (1907) pointed out, the principal diagnostic character for *Astatoreochromis* cannot be considered trenchant because some four-spined specimens of normally three-spined *Haplochromis* species have been recorded. He cites as an example an aberrant *H. desfontainesi* from Tunisia. Nevertheless, throughout the very numerous species of *Haplochromis* it is very exceptional to find an individual with more (or less) than three anal fin spines and as yet no specimens of *Astatoreochromis* with less than four anal spines have been found. It cannot be denied that *Astatoreochromis* and *Haplochromis* are closely related (as are *Haplochromis* and the other monotypic genera of Lakes Edward and Victoria) and it might seem that little is to be gained from recognizing *Astatoreochromis* as a distinct genus.

However, *Astatoreochromis* differs from the *Haplochromis* of Lakes Victoria and Edward in four other characters which, if taken together, may indicate that it has a different lineage from these species. In an earlier paper (Greenwood, 1954) I drew attention to the form of the pharyngeal apophysis in *Astatoreochromis* and showed that it resembles the apophysis occurring in *Haplochromis vanderhorsti* Greenwood (Malagarasi River) and *H. mahagiensis* David & Poll (Lake Albert). The other Victoria species with enlarged pharyngeal bones (*H. ishmaeli* Blgr. and *H. pharyngomylus* Trewavas) have a different apophyseal form. A summary of these observations is given in Text-fig. 2.

Contrary to my earlier views, I now consider that, taken by itself, apophyseal form is of doubtful value as an indicator of phyletic relationship. For example, both the *H. mahagiensis*-*H. vanderhorsti* and the *H. ishmaeli*-*H. pharyngomylus* types of apophysis are found in Lake Nyasa *Haplochromis* with enlarged pharyngeal bones; *Haplochromis placodon* Regan (a species with hypertrophied pharyngeals) has the "*ishmaeli*" type whilst *H. sphaerodon* Regan, *H. latistriga* (Günther) and *H. selenurus* (Regan) (species with less massive pharyngeals) have the "*mahagiensis*" type. There is no evidence to suggest that Nyasa fishes with "*mahagiensis*"-like apophyses are more closely related to one another than to *H. placodon*, or that they represent an exotic element within the Nyasa flock. Certainly there is no indication of their being related to the *H. mahagiensis*-*H. vanderhorsti* species group. Thus, one must conclude that similarity of apophyseal form is yet another example of convergent evolution, at least at an inter-group level.

Considering *Astatoreochromis* in relation to the cichlid species flocks of Lakes Victoria and Edward it is clear that this genus does not conform to the general morphological pattern of the endemic species and genera. Three characters, the shape of the caudal fin, the coloration and the high number of anal ocelli, set *Astatoreochromis* apart. Excepting *H. melanopterus* (a species of doubtful validity, see Greenwood, p. 192) all the endemic *Haplochromis* of Lake Victoria have a truncate or subtruncate caudal fin; the caudal of *Astatoreochromis* is distinctly rounded.

A considerable variety of colour and colour patterns is exhibited by the endemic

Haplochromis, but all can be broken down into various combinations of several basic types. The golden-green ground colour of *Astatoreochromis* does not occur in any endemic species. The third outstanding characteristic of *Astatoreochromis* is the high number of ocelli on the anal fin of male fishes. Not only are the ocelli more numerous than in *Haplochromis*, but they are arranged in three or four horizontal rows; it is extremely rare to find more than two rows in any *Haplochromis* from Lake Victoria or Edward.

In all these characters, *Astatoreochromis* resembles *H. vanderhorsti*. There is also one other point of close inter-specific resemblance; both species show only slight dimorphism in the coloration of the two sexes. In contrast the coloration of Lake Victoria *Haplochromis* is markedly dimorphic.

Thus, although the form of the pharyngeal apophysis alone is of doubtful value in showing phyletic relationships, I consider that the additional evidence supports my original conclusion that *Astatoreochromis* was derived from an *H. vanderhorsti*-like stem. The two other Victoria species with enlarged pharyngeal bones and dentition (*H. ishmaeli* and *H. pharyngomylus*) are apparently related to one another. Their origin was probably by way of two forms represented in the present lake by a generalized species formerly confused with *H. michaeli* [see Greenwood, 1954 and 1956a], but now known to be an undescribed species and a species partly advanced towards extreme hypertrophy of the pharyngeal mill (*H. obtusidens*).

The apparently distinct origin of *Astatoreochromis alluaudi* in relation to the rest of the Victoria-Edward *Haplochromis* species flock is a further and perhaps more fundamental reason for maintaining the species as a distinct genus.

Astatoreochromis alluaudi Pellegrin, 1903

(Text-fig. 1)

For synonymy see under genus.

Lectotype. A female 122 mm. S.L. from the Kavirondo Gulf, Lake Victoria; Reg. No. 04, 137 of the Paris Museum.

Description. From the available material it seems that only two characters (length of the caudal fin and the extent to which the lower pharyngeal bones are hypertrophied) show clear-cut differences between populations inhabiting the various lakes. These two characters will be treated separately but all others are given for the species as a whole.

The general species description is based on the following material: Lakes Victoria and Kyoga (including the Victoria Nile), 77 specimens, 20–163 mm. S.L. (of which 40, including the four syntypes, were used in obtaining proportional measurements); Lakes Edward and George 11 specimens 24.0–80.0 mm. S.L.; Lake Nakavali, 18 specimens, 50–137 mm. S.L. (of which 11 were used for proportional measurements); Lake Kachira, three specimens 66–78 mm. S.L.

Depth of body 33.8–43.3 per cent of standard length, length of head 32.1–40.0, mean (M) = 35 per cent. Dorsal head profile fairly steeply sloping, straight or somewhat decurved, becoming concave in larger individuals.

Preorbital depth, showing slight positive allometry with standard length, 11.1–17.5 ($M = 15.0$) per cent of head length, least interorbital width 25.2–31.7 ($M = 28.3$) per cent. Snout as broad as long, its length 25.0–33.3 ($M = 29.2$) per cent of head. Eye diameter shows negative allometry with standard length, being 31.5–23.2 ($M = 27.2$) per cent of head in fishes 20–80 mm. S.L. and 24.3–18.8 ($M = 22.1$) per cent in larger individuals. Depth of cheek positively allometric with standard length; 12.8–26.0 ($M = 21.3$) and 20.0–27.9 ($M = 24.2$) per cent of head in the two size groups mentioned above.

Caudal peduncle 11.0–15.2 per cent of standard length, its length/depth ratio 1.0–1.4 (modal range 1.0–1.1) or, rarely, deeper than long.

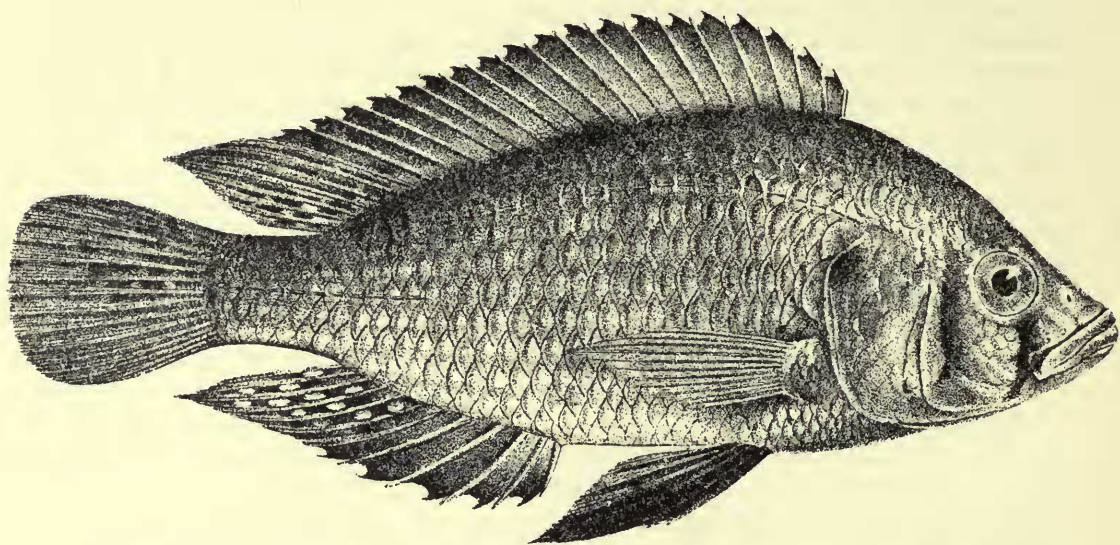


FIG. 1. *Astatoreochromis alluaudi alluaudi* (from Boulenger, *Fishes of the Nile*).

Mouth horizontal or slightly oblique. Jaws equal anteriorly or, occasionally, lower somewhat projecting; posterior tip of the maxilla reaching or almost reaching the vertical to the anterior orbital margin. Lower jaw 35.0–45.3 ($M = 40.0$) per cent of head length and 1.3–2.0 (rarely) times as long as broad (modal range 1.5–1.6).

Gill rakers short and stout; 8 or 9 (occasionally 10, rarely 7) on the lower limb of the first gill-arch.

Scales ctenoid; lateral line with 30 (f.12), 31 (f.21), 32 (f.20) or 33 (f.2) scales; cheek with 3 or 4 (occasionally 5) series; 4 or 5 (occasionally 6) scales between the origin of the dorsal fin and the lateral line; 4–6 (rarely 7) between the pectoral and pelvic fin bases.

Fins. Dorsal with 23 (f.2), 24 (f.4), 25 (f.15), 26 (f.68), 27 (f.11) or 28 (f.1) rays, comprising 16 (f.5), 17 (f.16), 18 (f.59), 19 (f.20) or 20 (f.1) spinous and 7 or 8 (rarely 9) branched rays. Anal fin with 11 (f.3), 12 (f.67), 13 (f.30) or 14 (f.2) rays comprising

4 (f.28), 5 (f.63) or 6 (f.11) spinous and 7 or 8 (rarely 6 or 9) branched rays. Pectoral fin shorter than the head, 22.3–29.4 per cent of standard length.

Caudal fin rounded, longer in fishes from Lakes Nakavali, Edward and George than in those from Lake Victoria; namely: length of caudal fin in Victoria specimens ($N = 41$) 21.4–28.5 (Mean 24.3) per cent of standard length; in Lake Nakavali fishes ($N = 4$) 24.0–31.6 ($M = 27.4$) per cent, and in Lake Edward fishes ($N = 9$), 24.0–31.6 ($M = 27.0$). This fin was damaged in two of the three specimens from Lake Kachira.

Pelvic fin with the first ray produced and extending to beyond the vent or as far as the spinous part of the anal fin.

Teeth. Even in the smallest specimen examined, the most posterior teeth in the upper jaw were unicuspid. In fishes less than 100 mm. S.L., the anterior and lateral teeth of the upper jaw and the entire outer series of teeth in the lower jaw are unequally bicuspid and relatively stout. In larger specimens, the dentition is a mixture of weakly bicuspid and unicuspid teeth; fishes over 140 mm. S.L. (and some smaller individuals) have only stout, unicuspid teeth in the outer series of both jaws. There are 28–56 (modal range 40–46) outer teeth in the upper jaw.

The small, tricuspid or unicuspid inner teeth are arranged in one or two rows.

Osteology. *Vertebrae*: 15 + 14 in the single specimen examined B.M. (N.H.) Reg. No. 1911.3.3.111, from Kakindu, Victoria Nile.

Neurocranial apophysis for the upper pharyngeal bones. The form of this apophysis was mentioned in the discussion on generic characters. Since the apophysis is of importance in defining cichlid genera, its variation and the probable factors influencing its variability in *Astatoreochromis* will be outlined briefly.

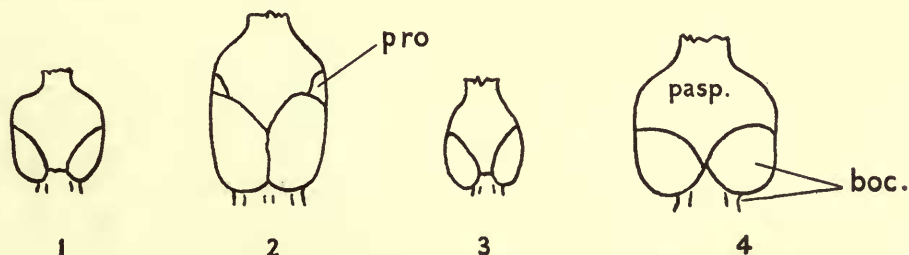


FIG. 2. Semi-diagrammatic representation of the shape and proportions of elements contributing to the upper pharyngeal apophysis in: (1) young *Astatoreochromis a. alluaudi*; (2) adult *A. a. alluaudi*; (3) adult *Haplochromis vanderhorsti*; (4) adult *Haplochromis ishmaeli*. Scale constant.

Although the shape and proportions of elements contributing to the apophysis are affected by the relative size of the pharyngeal bones, the characteristic group facies (see p. 170) is developed even in the absence of markedly hypertrophied pharyngeals (Text-fig. 2, (i)). In *A. alluaudi* it appears that the extent to which the basioccipital facets are enlarged and expanded depends primarily on the relative hypertrophy of the pharyngeals, and secondarily on the size of the fish. Thus, in

two specimens from Lake Victoria, one, 73 mm. S.L. with weakly developed pharyngeals, has proportionately smaller basioccipital facets than the other, 63 mm. S.L. and with enlarged pharyngeal bones and teeth (cf. Text-fig. 2 (i) and 2 (ii)). Likewise, fishes 70 mm., 76 mm., and 80 mm. S.L., from Lake Edward, and two specimens 71 mm. and 82 mm. S.L. from Lake Nakavali all have weakly developed pharyngeals, and apophyses comparable with the 73 mm. fish mentioned above. In this size-range it would appear that the size of the pharyngeal bones is exerting full influence on apophyseal form.

The effect of overall size is demonstrated in a fish 125 mm. S.L. from Lake Nakavali. In this specimen the pharyngeal bones are weak in comparison with those of a comparable sized fish from Lake Victoria (cf. Text-fig. 3, lower row, left and right). Yet, the apophyseal form is similar in the two specimens except for a slightly smaller surface area in the Nakavali fish.

Lower pharyngeal bone triangular. The form of this bone (which depends on the degree to which it is hypertrophied) and the nature of its teeth show a marked difference between fishes from Lake Victoria (including Kyoga) and those from the other lakes (see Text-fig. 3). When specimens of equal sizes from different lakes are compared it is immediately obvious that those from Lake Victoria have more massive bones with a greater proportion of molariform teeth. As far as can be determined from available material there is a little geographical variation of this character in fishes from Lakes Edward, George, Nakavali and Kachira. In all these populations the bone is clearly less massive than in Lake Victoria fishes and there are fewer molariform teeth. When present, such teeth are generally confined to the two median rows; any enlarged teeth in the lateral series are usually cuspidate.

The difference in pharyngeal bone size can be expressed quantitatively by using the ratio of head length to pharyngeal bone width (measured from tip to tip of the upper arms); it is, however, less impressive an indication of disparity in massiveness than an actual comparison of individual bones. The ratio for specimens from the various lakes is: *Victoria* (including Kyoga): 2.4-3.1 (Mean 2.7; 32 specimens examined); *Nakavali*: 2.6-3.6 (Mean 3.1; 16 specimens); *Edward and George*: 2.8-3.6 (Mean 3.0; 10 specimens); *Kachira*: 2.7-3.1 (Mean 3.0; three specimens).

As specimens of *A. alluaudi* from Lake Victoria cover a sufficiently wide size-range it is possible to determine ontogenetic changes in tooth form and in the proportions of the bone. In the smallest specimen (20 mm. S.L.) the two median tooth-rows are composed of enlarged but cuspidate teeth and the bone is relatively coarse (Text-fig. 3 top row, left). With increasing size, the bone becomes proportionately stouter and the median teeth larger and blunter (Text-fig. 3 middle row, left), as do some of the teeth in the lateral rows. In the great majority of fishes over 60 mm. S.L., only the most lateral series of teeth, and those in the upper corners of the bone, remain slender and cuspidate. The number of such non-molariform teeth is even further reduced in fishes greater than 120 mm. S.L. Only seven of the 78 fishes examined had pharyngeal bones and dentition less hypertrophied than the modal condition for their respective size-groups.

Ontogenetic changes are less marked in *A. alluaudi* from the western lakes. The impression gained from these specimens is that the pharyngeal bones, apart

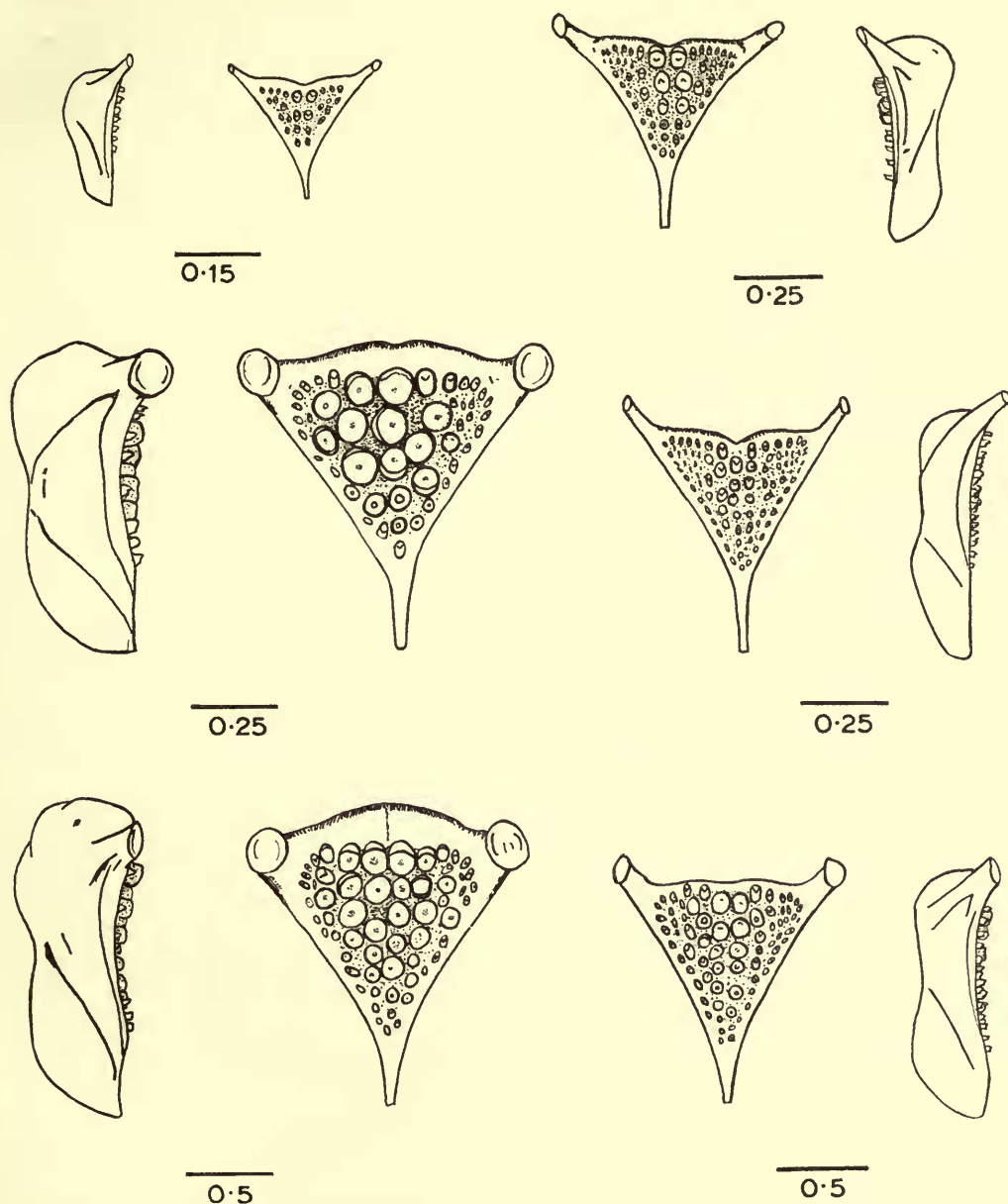


FIG. 3. Lower pharyngeal bones and teeth (lateral and occlusal views) of: Top row, left *Astatoreochromis a. alluaudi* 20 mm. S.L.; right, *A. a. alluaudi* 48 mm. S.L. Middle row, left, *A. a. alluaudi* 60 mm. S.L.; right, *A. a. occidentalis* (Lake Nakavali) 63 mm. S.L. Bottom row, left, *A. a. alluaudi* 120 mm. right, *A. a. occidentalis* (Lake Nakavali) 123 mm. S.L. Scale in centimetres.

from their greater size, may be compared with those of 20–30 mm. *A. alluaudi* from Lake Victoria.

Nothing is known about the epigenetics of *A. alluaudi* and little is known of the feeding habits of populations in lakes other than Victoria. It is therefore impossible to define the causal factors for the marked intra-specific, geographical difference in pharyngeal bones and teeth.

In Lake Victoria, *A. alluaudi* feed almost exclusively on Mollusca (see below) and particularly on the thick-shelled *Melanoides tuberculata*. Considering the extreme plasticity of bone and its response to intermittent pressure (see Murray, 1932; Weinmann & Sichner, 1947) it seems probable that the effects of crushing such prey might produce an adaptational thickening and strengthening of the pharyngeals. In this way, any genetical tendency towards pharyngeal hypertrophy (as manifest in the relatively coarse lower pharyngeals of post-larval *A. alluaudi*) would be reinforced. If, on the other hand, in the western lakes the species is not predominantly a mollusc eater, the adaptational stimulus for increased bone size would be less, and the bones might be relatively weak. Finally, the possibility of inter-populational genetic differences cannot be discounted, especially since the various lakes are geographically isolated.

Some data seem to add weight to the first, i.e. adaptational, hypothesis. The stomach and intestinal contents of 13 Lake Nakavali fishes have been examined; of these, two were empty. Five of the remaining 11 fishes had fed on small cichlid fishes, and six on bottom debris (plant tissue) and insects (both adult and larval). Despite a careful search, no remains of Mollusca were identified. Admittedly, 13 specimens do not constitute an adequate sample, but, if 13 Lake Victoria *A. alluaudi* in the same size-range were examined, every specimen with intestinal contents would have yielded remains of Mollusca.

Likewise, in four *A. alluaudi* from Lake Edward and one from Lake George, the predominant food was insects, although three individuals had scanty remains of small Gastropoda in the intestines. The snails could not be identified, except in so far as they were not *Melanoides* sp.

Coloration in life (known only from Lake Victoria). Sexual dimorphism is less marked in this species than in *Haplochromis* and the other monotypic genera. *Females and immature males*. Ground colour golden, overlain with olivaceous green, becoming yellow ventrally; a dark band runs obliquely downwards through the eye and becomes continuous with the lachrymal stripe, which runs obliquely backwards to the anterior tip of the preoperculum; often another dark band along the vertical limb of the preoperculum. All median fins olivaceous-yellow, the dorsal and anal outlined in black; caudal maculate. Pectoral fins hyaline; pelvics faintly yellow or hyaline.

Breeding males. Coloration essentially that of females except that the spinous dorsal is suffused with maroon, as is the entire anal fin, and the soft dorsal is densely spotted with maroon maculae. Anal fin with numerous yellow ocelli arranged in three or four vertical and the same number of horizontal rows. Pelvic fins black, the first ray pearly. Cephalic markings usually more intense than in females.

Preserved material: Adult males. Ground colour greyish-brown to brown, lighter ventrally; five or six dark transverse bars, often interrupted ventrally, on the flanks; occasionally an interrupted mid-lateral stripe. Cephalic markings as described above. Soft dorsal fin and entire caudal maculate; lappets of spinous dorsal, margin of soft dorsal and entire margin of anal fin black. Pelvics black laterally, the first ray pearly. Ocelli on anal fin dark grey. *Females and immature males.* Ground colour as in males but lighter. Soft dorsal and entire caudal weakly maculate or immaculate. Cephalic markings fainter than in males. Anal fin without ocelli, but in some individuals a few, small, light spots occur in the position of the ocelli. Pectoral and pelvic fins hyaline.

Affinities. The relationship of *Astatoreochromis alluandi* to the other monotypic genera of Lake Victoria and to certain species of *Haplochromis* was discussed above. It only remains to consider Regan's suggestion that *A. alluandi* is "Near *H. gestri*, especially distinguished by the increased number of dorsal and anal spines and the large blunt pharyngeal teeth". (*Haplochromis gestri* is a synonym of *H. obesus* (Blgr.) (see p. 182).

With the information now available on the anatomy and ecology of both species, it is clear that *A. alluandi* and *H. obesus* are not closely related. *Haplochromis obesus* belongs to a group of endemic Lake Victoria species which has developed the highly specialized habit of feeding on the embryos and larvae of other cichlid fishes (p. 187.) *Astatoreochromis*, on the other hand, possesses the potentialities for developing into a highly specialized mollusc-eater, although one subspecies is apparently a generalized bottom feeder. Besides the morphological differences noted by Regan, there are marked dissimilarities in the dentition and jaws of the two species. On the scale of divergence found in the *Haplochromis* and related species occurring in Lake Victoria, *A. a. alluandi* and *H. obesus* must be placed in very distinct lineages.

Differences in caudal fin length and the form of the pharyngeal bones are sufficiently well-marked to warrant the recognition of two subspecies of *Astatoreochromis*, one occurring in Lakes Victoria and Kyoga (including the Victoria Nile), and the other in Lakes Edward, George, Nakavali and Kachira, and in the Semliki River.

Admittedly one of the characters distinguishing the two groups could be considered a response to environmental differences (see p. 172). On the other hand, the importance of geographical isolation must be recognized. At present, and probably for a considerable period in the past, the western group of Lakes (Edward, Nakavali and Kachira) have been isolated from Lake Victoria by extensive papyrus-swamp divides on the interconnecting river systems (see Worthington, 1932). Likewise, Lakes Kachira and Nakavali are isolated from Lake Edward by intervening papyrus-swamps. Thus, although *Astatoreochromis* is relatively tolerant of papyrus-swamp conditions (see p. 174) the existence of such extensive swamp divides must considerably reduce any gene flow between the different lakes. Unfortunately, there is insufficient material from Lakes Edward, Kachira and Nakavali to determine whether a distinct subspecies occurs in each lake. At present, therefore, only two subspecies can be recognized.

Astatoreochromis alluaudi alluaudi Pellegrin

Diagnosis. *Astatoreochromis a. alluaudi* differs from the other subspecies in having a more massive lower pharyngeal bone with a greater number of molariform teeth, see Text-fig. 3 (ratio of head length to width of lower pharyngeal bone 2.4–3.1, Mean 2.7), and in having a shorter caudal fin (21.4–28.5 [Mean 24.3] per cent of standard length).

Other, ecological differences will be discussed below.

Distribution. Lakes Victoria, Kyoga and the Victoria Nile.

Astatoreochromis alluaudi occidentalis subsp. nov.

Type specimen. A male, 125 + 35.0 mm. long, B.M. (N.H.) Reg. No. 1933.2.23. 146, collected by Worthington from Lake Nakavali.

Diagnosis. Differs from the nominate subspecies in having a finer lower pharyngeal bone with fewer molariform teeth, see Text-fig. 3 (ratio of head length to width of lower pharyngeal bone 2.6–3.6, Mean 3.0) and in having a longer caudal fin (24.0–31.6, Mean 27.2 per cent of standard length).

Distribution. Lakes Edward, George, Nakavali and Kachira; the Semliki River above the rapids.

Ecology. Habitat. *A. a. alluaudi*, unlike the majority of *Haplochromis* species in Lake Victoria, is not confined to any particular type of substrate. Indeed, in this lake the subspecies is ubiquitous in all areas where the water is less than 60 feet deep. There are also indications that in Lake Victoria *A. a. alluaudi* may extend into deeper water. Graham collected one specimen in surface nets set over 193 feet of water some distance off-shore (Station 71; 0° 20½' S., 33° 1½' E.; in the collections of E.A.F.R.O. there is one other specimen caught by nets set on the bottom at ca. 180 feet (0° 4' S., 33° 14' E.).

During rainy seasons, post-larval *A. a. alluaudi* have been found in pools and streams some distance inside papyrus-swamps. Larger young (40–50 mm. S.L.) enter small temporary streams when these are flowing into the lake. Neither the papyrus-swamp habitat nor that of temporary streams is occupied by endemic *Haplochromis* or related species. Young and adults of the widely-distributed, fluviatile-lacustrine species *H. nubilus* (Blgr.) and *H. multicolor* (Schoeller) do, however, live in such habitats.

No habitat data are available for *A. a. alluaudi* in the Victoria Nile and Lake Kyoga, nor for *A. a. occidentalis* in any lake. Specimens of the latter have been collected from the Semliki River near its source in Lake Edward.

Food. *Astatoreochromis a. alluaudi* (Lake Victoria). The stomach and intestinal contents of 40 fishes (48–163 mm. S.L.) from different localities clearly indicate that *A. a. alluaudi* feeds almost exclusively on Mollusca, especially Gastropoda. In most of the specimens examined, some insect larvae were also found; but, both in volume and numbers, these represented only a small fraction of the ingested material. The very fragmentary nature of the shells found in the alimentary tract precluded

accurate identification of the mollusc species eaten. However, it seems most probable that the principal gastropod prey is *Melanoides tuberculata* (Müller), and the chief lamellibranch, *Corbicula* sp.

Astatoreochromis a. occidentalis. Lake Nakavali. Thirteen specimens 50–137 mm. S.L. were examined; two were empty. In the largest fish, the entire alimentary tract was filled with plant debris; five specimens (79–123 mm. S.L.) each contained fragmentary remains of small cichlid fishes (probably *Haplochromis*), with, in two, a little plant debris and some insect remains. The five smaller fishes (50–72 mm.) contained fragmentary insect remains (especially larval and adult Diptera) and plant debris.

Lake Edward. Only four specimens (62–76 mm. S.L.) were available for gut analysis; three contained a few unidentifiable fragments of mollusc shells together with bottom debris and the fourth (71 mm. S.L.), mostly adult insects (Diptera) and the very fragmentary remains of a small fish. Although the mollusc fragments could not be identified positively they were not derived from *Melanoides*.

Lake George. The alimentary tract of the single fish available (80 mm. S.L.) contained fragments of adult insects.

Lake Kachira. The three specimens examined (66–78 mm. S.L.) were all from one station and contained only bottom debris and plant remains (including water-lily seeds); a few fragments of insects were found in the intestine of one individual.

Breeding. Both subspecies of *Astatoreochromis alluaudi* are female mouth-brooders; exact spawning sites are not known. In Lake Victoria, males of *A. a. alluaudi* less than 100 mm. S.L. are immature but females are mature at about 95 mm. S.L. The three specimens of *A. a. occidentalis* from Lake Kachira (66–78 mm. S.L. 1 ♂ and 2 ♀) are all sexually active, thus suggesting that in this lake the subspecies reaches maturity at a smaller size than *A. a. alluaudi* in Lake Victoria. Little information was obtained on the size of sexually mature *A. a. occidentalis* in other lakes; a brooding female 57 mm. S.L. from Lake Nakavali and a ripe female 62 mm. long from Lake Edward seem to indicate that in these lakes female *A. a. occidentalis* also mature at a smaller size than do the females of *A. a. alluaudi* in Lake Victoria. It is possible that differences in the feeding habits of the two subspecies may be primarily responsible for the smaller adult size of *A. a. occidentalis*.

A marked disparity was noticed in the sex ratio of *A. a. alluaudi* from Lake Victoria and *A. a. occidentalis* from Lake Nakavali; there is insufficient material to determine the sex ratio in other localities. Using only those specimens whose sex could be ascertained with certainty, the ratio is 16 ♀: 46 ♂ in Lake Victoria, and 1 ♀: 7 ♂ in Lake Nakavali. Reasons for this discrepancy are obscure but at least any bias introduced by collectors selecting brightly coloured males can be discounted; both sexes are remarkably similar in colour. Furthermore, collections from Lake Victoria were made so as to eliminate this bias.

SUMMARY

1. The monotypic genus *Astatoreochromis alluaudi* is redescribed.
2. The generic characters are discussed, particularly from the phylogenetic viewpoint. It is thought that *A. a. alluaudi* was not derived from the same stem as other

Victoria and Edward species with hypertrophied pharyngeal bones and teeth. By the same tokens, *Astatoreochromis* is not closely related to the other and endemic monotypic genera of the two lakes. The genus is apparently related to such fluviatile species as *Haplochromis vanderhorsti* (Malagarasi River system) and *H. straeleni* (Congo system).

3. Two subspecific groups may be recognized, one from the Lake Victoria system and the other from lakes in western Uganda. These groups are given subspecific status, namely: *Astatoreochromis a. alluaudi* from Lakes Victoria and Kyoga, and the Victoria Nile; and *A. a. occidentalis* from Lakes Edward, George, Nakavali and Kachira, and the Semliki River.

4. The feeding habits of the two subspecies are described.

Study Material and Distribution Records.

<i>Astatoreochromis a. alluaudi</i>			
Museum and Reg. No.	Locality		Collector
	<i>Kenya</i>		
Paris Museum			
04,137	Kavirondo Bay	.	Alluaud
(Lectotype)			
04,138-9	" "	.	"
(Paratypes)			
B.M. (N.H.).—1904.6.281	" "	.	"
(Paratype, presented by Paris Museum)			
B.M. (N.H.).—1958.7.9.2	Kisumu Harbour	.	E.A.F.R.O.
	<i>Uganda</i>		
B.M. (N.H.).—1906.5.30.506-9	Entebbe	.	Degen
" 1906.5.30.505	Bunjako	.	"
" 1907.5.7.73-76	Buddu Coast	.	Simon
" 1911.3.3.112-3113	Jinja, Ripon Falls	.	Bayon
" 1958.7.9.3-5	Grant Bay	.	E.A.F.R.O.
" 1958.7.9.6	Karinya (near Jinja)	.	"
" 1958.7.9.7-16	Jinja	.	"
" 1958.7.9.18-21	Pilkington Bay	.	"
" 1958.7.9.22	Thruston Bay	.	"
" 1958.7.9.23	0° 4' S., 33° 14' E.	.	"
" 1958.7.9.24-37	Entebbe Harbour	.	"
" 1958.7.9.38	Beach nr. Nasu Point	.	"
" 1958.7.9.39-40	Stream at Bugungu,	.	"
	Napoleon Gulf		
" 1958.7.9.50	Ekunu Bay	.	"
" 1958.7.9.51-58	Ramafuta Island	.	"
	<i>Tanganyika</i>		
" 1958.7.9.1	Mwanza	.	"
" 1958.7.9.17	Majita	.	"
" 1958.7.9.41-49	Godziba Is.	.	"
	<i>Lake Victoria, Locality Unknown</i>		
" 1908.5.19.51	—	.	D. Radcliffe
" 1928.5.24.370-372	—	.	M. Graham

Museum and Reg. No.	Locality	Collector
	<i>Lake Kyoga and the Victoria Nile</i>	
„ 1911.3.27.21	Between Lake Kyoga and the Murchison Falls	F. Melland
„ 1911.3.3.108	Bululo, Lake Kyoga	Bayon
„ 1911.3.3.109-110	Kakindu, Victoria Nile	„
	<i>Astatoreochromis a. occidentalis</i>	
	<i>Lake Kachira</i>	
B.M. (N.H.).—1933.2.23.160-162		E. B. Worthington
	<i>Lake Edward</i>	
„ 1933.2.23.137-140		„
	<i>Lake George</i>	
„ 1933.2.23.141		„
	<i>Lake Nakavali</i>	
„ 1933.2.23.142-159		„

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